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THE CAMBALIDAE IN MEXICAN CAVES, WITH DESCRIPTIONS OF THREE NEW SPECIES OF *MEXICAMBALA* (DIPLOPODA: CAMBALIDA)

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Cambaloid millipedes, seldom collected in Mexico, are represented there by two families, the Cambalidae and the Leioderidae. The nearest relatives are the United States species of these families.

All known epigean cambaloid millipedes in Mexico have been assigned to three species of the family Leioderidae. They are scarce, none having been reported since the original descriptions were published (Loomis, 1968). I have new records of one of them, *Ergene setosus* Chamberlin, 1943, from a relatively small area in two northeastern states. Tamaulipas: C. Victoria, ♂; Hwy 85, Km 627–628, about 35 mi S of the Tropic of Cancer, ♂; El Venadito, Hwy 85, 8 mi S of Antiguo Morelos, ♂. San Luis Potosí: Hwy 85, 8 mi N of C. Valles, ♂. An immature female from El Tinieble, Hwy 25, Km 99, between Victoria and Matamoros, Tamaulipas, has fewer body setae than specimens from the previously listed sites and may represent another species. Immature specimens from Túxpan, Veracruz, probably represent an undescribed genus.

All known Mexican members of the Cambalidae are troglobites and can be assigned to either *Cambala* or *Mexicambala.* In Mexico, this family is much better known than the Leioderidae because of the zealous collecting by speleologists.

The troglobitic specimens reported on here were collected by members of the Association for Mexican Cave Studies, to

whom I am grateful for the opportunity of studying the material. Caves were located by using the maps of Russell and Raines (1967). Holotypes and paratypes of the new species described here have been deposited in the type collection of the National Museum of Natural History. The male holotype and female paratype of *Mexicambala russelli* Causey, 1964, are in the American Museum of Natural History. The remaining specimens are in my collection.

Key to the Mexican Cambalidae Based on the Male

1. Sides of collum are low and slightly flared, allowing antennae to fit under anterior margin; dorsal crests are not notched; peritremes are no higher than dorsal crests; viewed from above, paraprocts are slightly visible ectad of epiproct; apical margin of coxite of anterior gonopods is broad and slightly concave, and sternite is longer than wide ..... *Cambala speobia*

1′. Sides of collum are high, not flared, and have a notch in which margin of vertex articulates; dorsal crests have 1 or 2 notches, dividing them into 2 or 3 angular or rounded teeth; peritremes are higher than dorsal crests; viewed from above, paraprocts are not visible ectad of epiproct; apex of coxite of anterior gonopods is narrowed and rounded, and sternite is wider than long 2

2. Maximum length is about 34 mm; dorsal crests have 3 conspicuous angular teeth; peritremes are conspicuous and subcylindrical; apex of epiproct is rounded and asetose; paraprocts have setae (about 9) along mesial margin only; telopodite of anterior gonopods is as long as coxite ..... *Mexicambala fishi* new species

2′. Maximum length is about 26 mm or less; teeth (2 or 3) of dorsal crests are either rounded or angular and are less conspicuous; peritremes (either conical or subcylindrical) are less conspicuous; apex of epiproct is either rounded or peglike and either setose or asetose; few to many setae are scattered over paraprocts; telopodite of anterior gonopods is distinctly shorter than coxite 3

3. Dorsal crests have 2 notches, and teeth are mostly angular; peritremes are subcylindrical; apex of epiproct is rounded and asetose ..... *M. russelli*

3′. Dorsal crests have 1 notch, and teeth are mostly rounded; peritremes are either subcylindrical or conical; apex of epiproct is varied 4

4. Peritremes are usually high and conical; apex of epiproct bears a conspicuous setose peg ..... *M. blandus* new species

4′. Peritremes are lower and subcylindrical; apex of epiproct is rounded and seldom is setose ..... *M. inopis* new species

Genus *Cambala* Gray

Cambala.—Causey, 1964.—Shear, 1969.
Mexicambala.—Shear, 1969.

This predominantly epigean North American genus also has troglophilic and troglobitic species. The only Mexican record is of *C. speobia*, from a cave which drains into the Río Grande. It is improbable that additional search will extend the range significantly into Mexico.

Cambala speobia (Chamberlin)

Figures 1a, 2a

C. speobia.—Causey, 1964.

Diagnosis: A troglobitic species characterized by absence of ocelli and details of gonopods.

An occasional immature specimen has one or more ocelli. Mature males have a conspicuous, rounded lobe on ventral surface of article 4 of legpairs 6 and 7. Legpair 1 has pretarsi. Segments 2 and 3 have no traces of dorsal crests, which begin on segment 4. Peritreme-pore crests and 4 dorsal crests are on all remaining segments; none have distinct notches (Fig. 1a). Ventral crests are represented by some 18 to 20 distinct but narrow ridges. Apex of epiproct is rounded; from a dorsal view paraprocts are slightly visible lateral to epiproct. Each paraproct has 2 setae on its mesial margin. Local variations in body length are common; maximum is about 33 mm. Specimens from La Cueva de los Lagos tend to be small, with maximum length about 19 mm.

C. speobia occurs in many caves in the Edwards Plateau of central and southwest-central Texas (Causey, 1964). Bull and Mitchell (in press) pointed out that they are all either in the Balcones Fault or are within 50 miles of the Fault and postulated that the ancestors of *C. speobia* survived in the epigeum after the early Pleistocene. No other cambaloid millipede is troglobitic in the Edwards Plateau. The shorter legs and antennae of *C. speobia* suggest that this species did not become troglobitic as early as species of *Mexicambala* did.

Record of C. speobia *in Mexico*: Coahuila: Cueva de los Lagos, 15 mi. W of Acuña, 2 mi. S of the Río Grande; many specimens, 24 Jan. 1964, 14 Nov. 1964; J. Reddell, D. McKenzie, T. Raines. This cave was later flooded by the Amistad Reservoir. The polydesmoid genus *Speodesmus*, which is usually represented in Edwards Plateau caves with *C. speobia*, was not collected.

Genus *Mexicambala* Causey

Mexicambala Causey, 1964.
Cambala.—Shear, 1969.

Shear (1969), who regards *Mexicambala* as a junior synonym of *Cambala*, has ignored the well-defined somatic and sexual characters which separate the two species groups composing these genera.

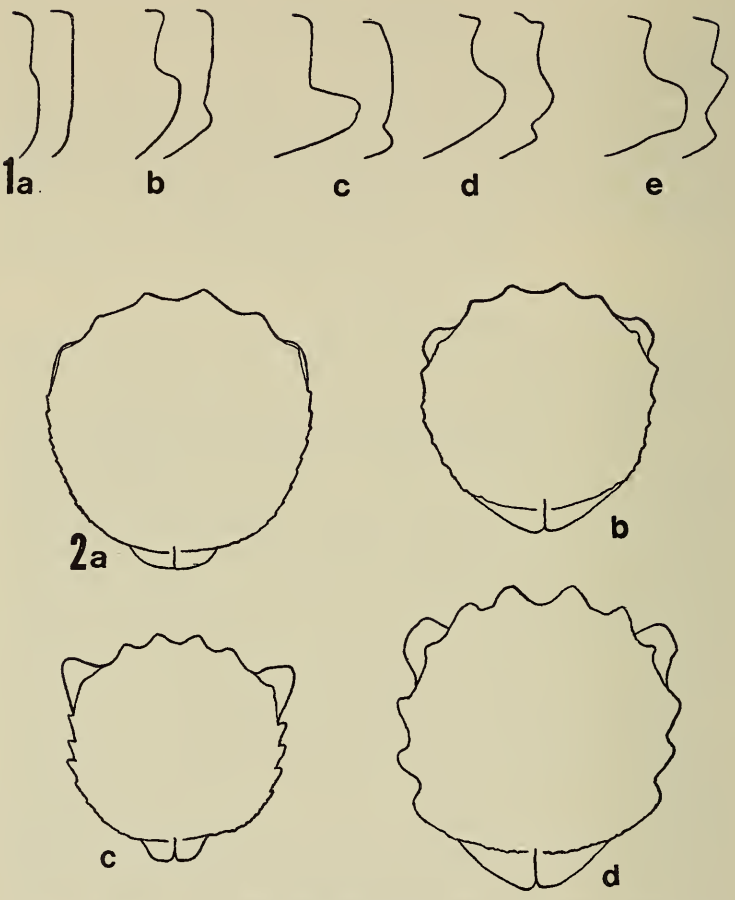

Fig. 1. Lateral view of peritreme-pore crest (first in each pair) and dorsal crest (second in each pair) of middle body segments. a, *Cambala speobia*; b, *Mexicambala inopis*; c, *M. blandus*; d, *M. russelli*; e, *M. fishi*.

Fig. 2. Caudal margin of segment 7 of male. a, *Cambala speobia*; b, *Mexicambala blandus*; c, *M. russelli*; d, *M. fishi*. From this view, *M. inopis*, which is not shown, is essentially like *M. russelli*.

Diagnosis: Eyeless, troglobitic, small cambalids characterized by prominent peritremes and notched dorsal crests. Near *Cambala*, differing as follows: sides of collum are higher, closer to head, and have a notch in which margin of vertex articulates; antennae are longer, reaching to segment 5, and have large sensory areas on distal margin of articles 5 and 6; dorsal crests are divided by 1 or 2 notches into 2 or 3 rounded

or angular teeth; epiproct covers paraprocts when viewed from above; apical margin of coxite of anterior gonopods is narrowly rounded and undivided.

Length 21–26 mm, segments 39–47. In life, depigmented except for red stink pores; in alcohol, flesh colored or grayish, quickly losing red pigment. Body is slightly narrowed behind head. Segment 7 of male is not swollen. Collum is length of segments 2 and 3; dorsal surface is smooth. Segments 2 and 3 have well-developed, slightly developed, or no crests. Segment 4 has well-developed crests without notches. Dorsal crests of segment 5 may have notches. By segment 9 crests have reached their maximum size and typical shape (Fig. 1b–d). Pores and pore crests begin on segment 5; distal part of pore crests is thin, resembling dorsal crests; anterior part with pore (peritreme) is either subcylindrical or conical and much higher than dorsal crests (Fig. 2b–d). Crests are lower on last 2 segments and absent on epiproct. Surface between crests is smooth and shining. Some 5 to 8 lateral crests, much thicker than in *Cambala*, are below pore crests; all or only upper ones may have 1 tooth, which is in line with middle tooth of dorsal crests. Apex of epiproct is either rounded or produced in a prominent peg with several setae. Paraprocts have a few setae along mesial margins only or scattered over their surface. Legpair 1 has pretarsi. Mature males have rounded lobes on ventral surface of article 3 and 4 and sometimes 5 of legpairs 6 and 7. Pretarsus of male is approximately one-half as long as tarsus, and in female it is one-third as long.

From an anterior view, apical region of telopodite of anterior gonopods is narrowed less than coxite; from a lateral view, telopodite is usually blunt and wider than coxite; sternite is shorter than it is wide from an anterior view (Figs. 3c, 4b). Posterior gonopods (Fig. 3d) are essentially as in *Cambala*; as in all species of *Cambala*, telopodite is composed of 2 articles; division between articles is less distinct in *Mexicambala* than in *Cambala*.

Distribution: Caves in mountains of Tamaulipas, San Luis Potosí, and Oaxaca.

Species: 4.

Speciation: The species have a north-south range, with *inopis* the most northern, followed by *blandus*, *russelli*, and *fishi*. There is a clinal variation in the surface sculpture, suggesting that the lengthening of the peritremes and the enlargement and notching of the crests coincided with the southern movement of the genus. *M. fishi* is easily distinguished from the northern species by its stronger surface sculpture and gonopods. The three northern species, which have contiguous ranges, resemble each other in that they have identical gonopods and have setae scattered over the paraprocts rather than only along the mesial margins. They comprise the *russelli* superspecies, differing from each other in the development of the surface sculpture, the length of the epiproct, and the abundance of the setae on the paraprocts. These characters, although somewhat variable, are reliable enough to be used to separate the species. *M. blandus*

and *M. inopis* are especially variable, with the populations of some caves distinctive enough to be recognizable.

Mexicambala inopis new species

Figure 1b

Diagnosis: Distinguished from other members of the *russelli* superspecies by the relatively inconspicuous body sculpture. Resembles *M. russelli* in that apex of epiproct is rounded and peritremes are subcylindrical; differs in that there is only 1 notch on the dorsal crests.

Description of holotype: Male, length 22.5 mm, width 1.3 mm, segments 45. Articles 3, 4, and 5 of legpairs 6 and 7 have large ventral lobes. No dorsal crests are on segment 2. Dorsal crests are weakly indicated on segment 3. On segment 4, 10 distinct crests are on dorsum and sides. Dorsal crests of typical body segments have one small notch (first is on segment 9), and tooth in front of it is small and subangular (Fig. 1b). Peritremes are subcylindrical and relatively low. Lateral crests are low and number 6 to 8. Epiproct is rounded and lacks apical setae. Setae are scattered sparsely over paraprocts.

Gonopods are as in other members of the *russelli* superspecies.

Description of female paratype: Length 25.5 mm, segments 46. Setae are more numerous on paraprocts than in holotype.

Variations of paratypes from three caves: Length 20–33 mm, segments 34–46. No paratypes from Sótano de la Joya have setae or a swelling on the apex of the epiproct, and all have the dorsal crests as in the holotype. Specimens from the other 2 caves, which are nearer Rancho del Cielo, show a little intergradation with *M. blandus*. This is indicated by the slightly angular anterior tooth of the dorsal crests, the presence of a few setae on the epiprocts, and, in a female of 43 segments from Mine Cave, a slight swelling on the apex of the epiproct.

Range: Three caves within a distance of some 8 miles in the Sierra de Guatemala, southern Tamaulipas. This is northwest of and contiguous to the range of *B. blandus*.

Type locality and specimens: TAMAULIPAS: Sótano de la Joya de Salas, W of Rancho del Cielo about 6 mi.; 5 ♂, including holotype, 2 ♀; 3 June 1965, J. Fish, H. Russell.

Other localities and specimens: Cueva de los Leones, ♂, ♀; 5 June 1965, M. McKenzie. Mine Cave, 6 mi. NW of Gómez Farías, 1 immature, 9 Mar. 1966, J. Redell; ♂, ♀; 3 June 1967, R. Mitchell.

Deposition of specimens: Holotype (undissected) and ♀ paratype from type locality; paratypes of both sexes from Cueva de los Leones and Mine Cave; National Museum of Natural History.

Mexicambala blandus new species

Figures 1c, 2b, 3

Diagnosis: Distinguished from other members of the *russelli* superspecies by the peg on the apex of the epiproct and the prominent conical

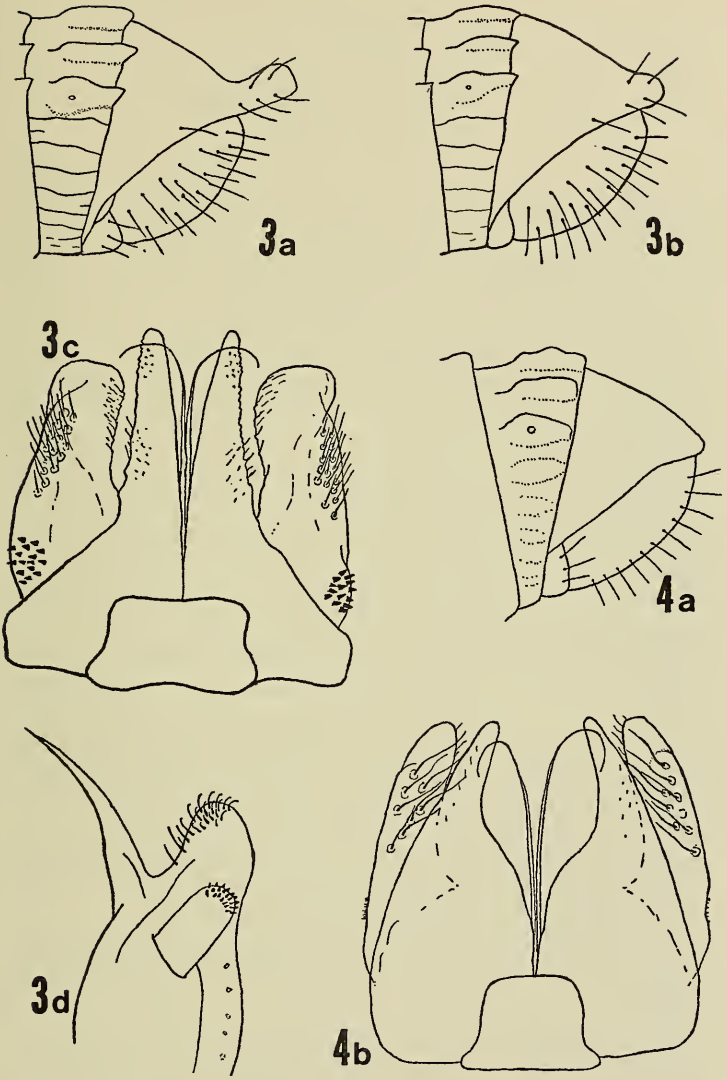

Fig. 3. *M. blandus.* a, hind end of female (Crystal Cave); b, hind end of female (Bee Cave); c, anterior view of anterior gonopods (Crystal Cave); d, subcephalic view of left posterior gonopod (Cueva del Agua).

Fig. 4. *M. fishi.* a, hind end of holotype; b, anterior view of anterior gonopods of paratype.

peritremes. Resembles *M. inopis* in that dorsal crests have only 1 small notch and are low.

Description of holotype: Male, length 18.5 mm, width 1.1 mm, segments 38. Thick, rounded lobes are on ventral surface of articles 3, 4, and 5 of legpairs 6 and 7. Crests are weakly indicated on segment 2. On segments 3 and 4 crests are well formed. Dorsal crests of typical segments have 1 small notch (first is on segment 7), which is preceded by a small, angular tooth and followed by a slightly convex ridge. Peritremes are conical, salient, with pore near apex. Most segments have 7 lateral crests, of which upper 3 are thickened. Caudal peg is setose, blunt, and a little shorter than peg of female shown in Fig. 3a. Setae are more sparsely arranged on paraprocts than in female.

Anterior gonopods (Fig. 3c) and posterior gonopods (Fig. 3d) are like those of other members of the *russelli* superspecies.

Description of female paratype from Harrison's Sinkhole: Length 23 mm, width 1.7 mm, segments 40. Surface sculpture is as in holotype. Caudal peg (Fig. 3a) is slightly longer and paraprocts are slightly more setose than in holotype.

Variations of paratypes from all localities: Length 18–23 mm, segments 38–43. The characters which are so conspicuous in this species, the caudal peg and conical peritremes, are largest in the northern part of the range in the caves at Rancho del Cielo. Both structures diminish in size along a north-south cline and reach their maximum reduction at Bee Cave, near Chamal (Fig. 3b, female of 40 segments).

The length of the caudal peg also varies ontogenetically and sexually. In the early stadia it is represented by setae and a thickened ridge, and it does not reach its maximum size until specimens have molted to about 40 segments. In mature females at Rancho del Cielo the peg tends to be from one-fourth to one-third longer than in mature males. In the southern part of the range the sexual variation in the length of the caudal peg is less marked because the peg is so much shorter there.

Range: Six caves with a north-south range of 21 miles in the Sierra del Abra of southern Tamaulipas. This is between the ranges of *M. inopis* to the northwest and *M. russelli* to the south.

Type locality and specimens: TAMAULIPAS: Harrison's Sinkhole, Rancho del Cielo, 1♂, 2♀, 5 June 1964, on decaying organic matter, J. Reddell et al.; 7♂, including holotype, 30♀, 25 Mar. 1967, R. W. Mitchell.

Other localities and specimens (in order of north-south distribution): TAMAULIPAS: Crystal Cave, Rancho del Cielo, ♂, ♀, immatures, Aug. 1966 and Mar. 1967, R. W. Mitchell; ♂, ♀, June 1964, J. Reddell et al. Sótano de Gomez Farías, 6 mi. NW of Gomez Farías, ♂, ♀, 12 June 1964; 6 Dec. 1964, T. Raines. Cueva del Nacimiento del Río Frío, 3 mi. S of Gómez Farías, ♀, 11 Mar. 1969, J. Reddell. Bee Cave, 6 mi. N of Chamel, ♂, ♀, 29 Jan. 1968 and 26 May 1968, J. Reddell. Grutas del Puente, 5 mi. SE of Ocampo, ♂, ♀, 13 July 1967, J. Reddell.

Deposition of specimens: Holotype (undissected) and paratypes of both sexes from Crystal Cave and Bee Cave; National Museum of Natural History.

Mexicambala russelli Causey

Figures 1d, 2c

M. russelli Causey, 1964.

Diagnosis: Distinguished from other members of the *russelli* superspecies by the more angular middle tooth of the dorsal crests. Resembles *M. inopis* in that apex of epiproct is rounded and peritremes are subcylindrical; differs in that surface sculpture is more strongly developed and setae are more numerous on paraprocts.

Length 20–26 mm, width 1.3–1.6 mm, segments 38–45. Lobes on leg-pairs 6 and 7 are smaller than in *M. inopis*. Dorsal crests are very faintly developed on segments 2 and 3 and a little more strongly on segment 4; by segment 8 they have their typical form (Fig. 1d). Most segments have 8 lateral crests; upper one has a small middle tooth. Surface sculpture is most like that of *M. fishi*, differing in that peritremes and teeth of dorsal crests are a little smaller and lateral crests are much smaller. Apex of epiproct is rounded and asetose; paraprocts are most thickly setose of genus.

Anterior gonopods are as shown for *M. blandus* (Fig. 3a). The previously published figure (Causey, 1964) shows apex of telopodite too broad; apex normally has this appearance from a lateral view, but from an anterior view apex appears broad only when pressure is applied. Posterior gonopods are as in congeners.

Range: Eight caves in the Sierra Madre Oriental in the vicinity of Aquismón and Xilitla, eastern San Luis Potosí. North-south extent of range is 24 miles. Nearest congener is *M. blandus*, some 108 miles north.

Type locality: San Luis Potosí: Cueva de la Parra, 3 mi. N of Xilitla.

Other localities and specimens (in order of north-south distribution): Cueva de San Miguel, 10 mi. W of Aquismón, ♂, ♀, immatures, Sept. 1967, J. Fish and W. Russell. Cueva del Agua, 8 mi. NW of Aquismón, ♂, ♀, April 1964, W. Russell. Cueva de Ahuate #2, 1.5 mi. SW of Xilitla, ♀, 7 June 1964, D. McKenzie and J. Reddell. Cueva del Salitre, Xilitla, ♂, ♀, 24 April 1966, T. Raines. Cueva de Poca Ventana, 0.6 mi. W of Xilitla, ♀, Jan. 1968, T. Raines. Sótano de Tlamaya, near Xilitla, ♀, 31 July 1964, 8 July 1967, T. Raines. Cueva de Potrerrillos 1 mi. W of Ahuacatlan, ♂, 12 July 1967, J. Reddell et al.; ♀, 25 Nov. 1967, J. Fish.

Deposition of specimens: Holotype (undissected) and female paratype, American Museum of Natural History (New York). Topotypes and specimens of both sexes from La Cueva del Agua, National Museum of Natural History.

Mexicambala fishi new species

Figures 1e, 2d, 4

Diagnosis: Characterized by gonopods and very conspicuous surface sculpture. Resembles *M. russelli* in that middle tooth of dorsal crests is angular; differs from all congeners in that telopodite of anterior gonopods is as long as coxite, paraprocts have setae only along mesial margin, and body is larger.

Description of holotype: Male, length 33 mm, width 1.8 mm, segments 46. Articles 3 and 4 of legpairs 6 and 7 are slightly enlarged. Distinct crests are on dorsum and sides of segments 2, 3, and 4. Dorsal crests of segment 5 and all following segments have 2 notches. On typical segments teeth of dorsal crests are large and angular and peritremes are high and cylindrical (Figs. 1e, 2d). On most segments there are 5 lateral crests, each one with a thick, blunt middle tooth. Apex of epiproct is rounded and asetose; paraprocts bear 9 setae along mesial margin (Fig. 4a).

Anterior gonopods are characterized by relatively long and apically narrowed and rounded telopodite; from a lateral view apical region of telopodite is rounded and about as broad as from anterior view. On posterior surface of distal one-third of coxite there is a series of short setae; there are longer setae, 8 or 9 in 2 irregular series, on both anterior and posterior surfaces of distal one-half of telopodite. Posterior gonopods are as in congeners.

Description of female paratype: Length 34 mm, width 2.1 mm, segments 47. Surface sculpture is as in holotype.

Variations of paratypes: 6 males: length 24–33 mm, segments 43–46. 14 females: length 30–36 mm, segments 43–47.

Range: Known only from the type locality in the mountains of northern Oaxaca. This is about 265 miles south of the nearest collection site of *M. russelli*.

Type locality and specimens: Oaxaca: Cueva Arriba de Río Iglesia, 4 mi. E Huautla, lat 18°20′ N, long 96°45′ W, 1700 m alt; 7 ♂, including holotype, 14 ♀, 3 immatures; J. Fish, H. Russell.

Deposition of specimens: Holotype (undissected), 3 ♂ paratypes, 8 ♀ paratypes, National Museum of Natural History.

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